BREEDING BIOLOGY OF THE LESSER SANDHILL CRANE *GRUS CANADENSIS CANADENSIS* (L.) ON THE YUKON-KUSKOKWIM DELTA, ALASKA

A

THESIS

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BREEDING BIOLOGY OF THE LESSER SANDHILL CRANE

GRUS CANADENSIS CANADENSIS (L.)

ON THE YUKON-KUSKOKWIM DELTA, ALASKA

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ABSTRACT

Parameters of the breeding biology of the Lesser Sandhill Crane on the Yukon-Kuskokwim Delta, Alaska, were studied to assess their relationship to the welfare of the population. During summers of 1975 and 1976, nests were located and monitored, chicks were marked, and birds were observed from towers and blinds. Chicks were color-banded prior to fledging. Twenty-six nests were located in sedge/grass meadow and heath/marsh mosaic habitats. Nesting density was 0.54 nests/km^2 in 1975 and 0.78 nests/km^2 in 1976. Hatching success was 63.6% and nesting success was 66.7% each year. In 1976, 71% of chicks survived to fledging and mean brood size was 1.3, compared with 56% survival and mean brood size of 1.0 in 1975. Overall density was 1.5 cranes/km^2, with most birds observed in sedge/grass meadow. Ten of 90 color-marked cranes were resighted during migration and on wintering areas.

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INTRODUCTION

Lesser Sandhill Cranes (*Grus canadensis canadensis* L.) (bird names according to American Ornithologists' Union 1957) breed from northern Alaska, Banks Island and Baffin Island south to Cook Inlet (Alaska), southern Mackenzie, southern Keewatin and Southhampton Island (American Ornithologists' Union 1957). Observations of Lesser Sandhills on their breeding grounds were reported by Nelson (1887), Conover (1926), Warburton (1931), Brandt (1943), Walkinshaw and Stophlet (1949), Dement'ev and Gladkov (1951), Gabrielson and Lincoln (1959), Kessel et al. (1964) and others. Most of these reports, however, were restricted to a few days' observation. No comprehensive study of this subspecies' breeding biology has been conducted to date.

The 69,000 km^2 Yukon-Kuskokwim Delta, located between the lower Yukon and Kuskokwim Rivers, is "a patchwork of low, marshy tundra interspersed with thousands of small ponds" (Spencer et al. 1951). This area supports more Lesser Sandhill Cranes than any other region in Alaska (King and Lensink 1971). Density and habitat requirements of cranes on the Delta have not been investigated, and specific migratory pathways and wintering areas of these birds are not known.

Sandhill Cranes are hunted in nine states, two Canadian provinces and Mexico. Lesser Sandhills comprise the majority of the hunted population and an estimated 15,000 or more cranes are harvested annually (Wilson Ornithological Society 1975). Yet little is known of the Lesser Sandhill Crane's reproductive potential due to lack of information from breeding-ground study.

The objectives of this study were to (1) investigate Lesser Sandhill Crane breeding biology parameters including nesting density, nesting dates, mean clutch size, hatching success, and survival of chicks to fledging and (2) examine density and distribution by habitat type of the population throughout the summer. A Sandhill Crane banding and color-marking program, initiated with this study and being continued as a Clarence Rhode National Wildlife Range program, is intended to provide marked cohorts for investigation of (1) migratory routes and wintering areas of cranes from the Yukon-Kuskokwim Delta, (2) age of first reproduction of the Lesser Sandhills and age-specific breeding success, and (3) the relationship, if any, among crane populations in Alaska and Siberia.

The study was conducted on Clarence Rhode National Wildlife Range from 12 June through 20 August 1975 and 2 May through 1 September 1976. Additional information was obtained from the Refuge files and from C. P. Dau, J. Heather, the International Crane Foundation, M. R. Petersen, P. G. Mickelson and D. G. Raveling.

METHODS AND MATERIALS

Study Area

The study area is centered at Old Chevak (61°26'N, 165°27'W) on the Clarence Rhode National Wildlife Range on the Yukon-Kuskokwim Delta, 24 km from the Bering Sea coast near the village of Chevak, Alaska (Figure 1). The Kashunuk and Keoklevik Rivers are the major waterways transecting this area. Many tidal sloughs draining into the rivers, and numerous ponds and small lakes make most land accessible by boat (at certain tides) or small aircraft. Vegetation types are wet marsh tundra and heath tundra, as described by Holmes and Black (1973), sedge/grass meadow (Mickelson 1973; Dau 1974), and pond shore vegetation (Petersen 1976). Heath and wet marsh tundra form a mosaic pattern of low, wet marshes broken up by raised heath tundra. In both years of the study, tracts of sedge/grass meadow and heath/marsh mosaic were included in the study area. Only 16.6 km^2 were studied in 1975 due to my late arrival on the study area. In 1976, however, the area was expanded to 26.9 km^2 in order to increase the number of nests studied.

Breeding Birds

Throughout the season, towers 3.3 to 4.9 m tall, nylon blinds and small boats were used as vantage points from which to observe general activities, location of chicks, size of broods, behavior, and phenology.

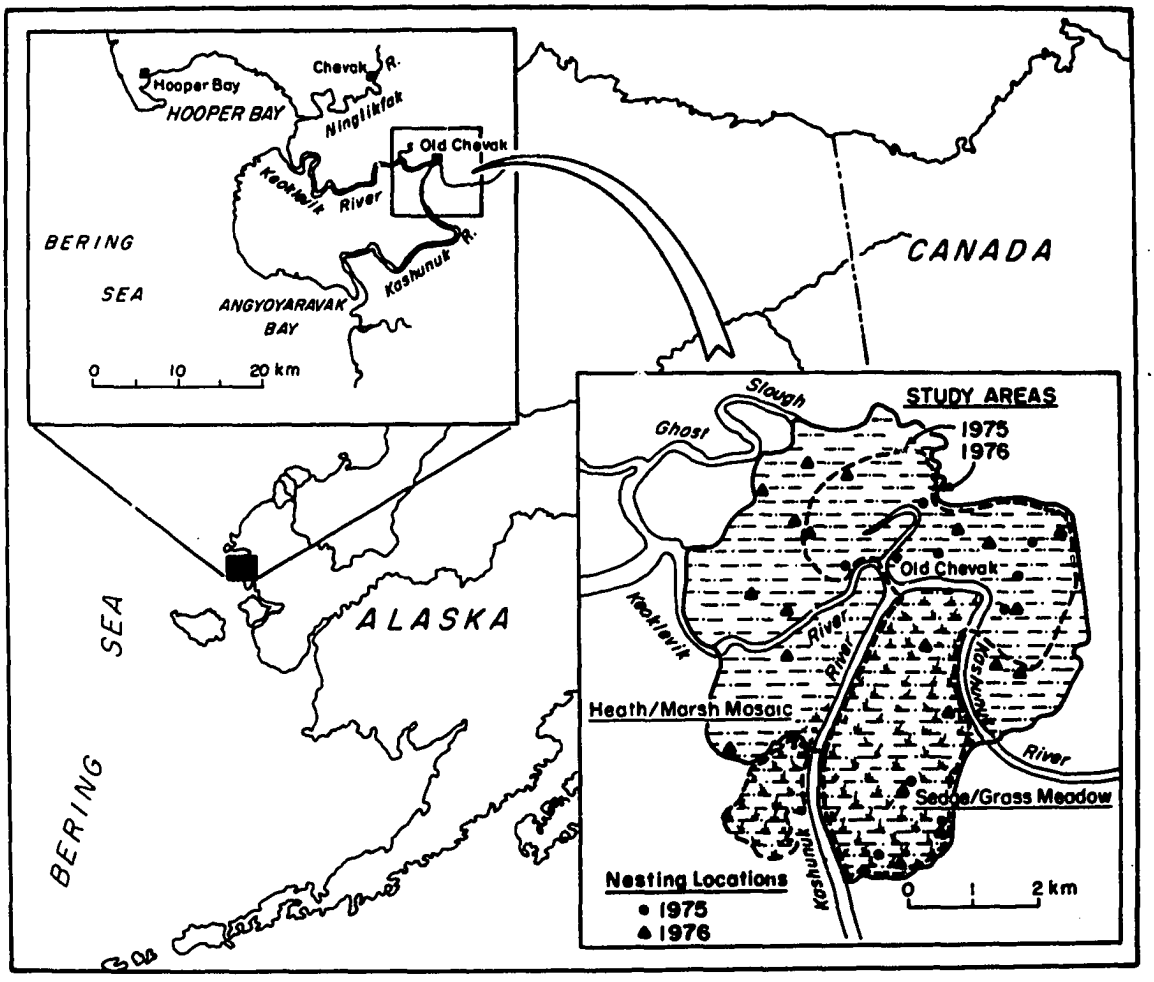

Figure 1. Study area on the Yukon-Kuskokwim Delta, Alaska.

Territorial pairs were watched and nests located from my arrival until first hatching in both years. Within pairs, male and female were identifiable by unison call (Walkinshaw 1965a). In 1976, pair locations were mapped daily in order to facilitate nest location later. Systematic walking of the study area to locate nests began on 13 June 1975 and, in 1976, on 1 June, when most if not all breeding birds had established nests. The location of each nest was marked on a map (scale 1:63,360 or 1:10,560). Nests were visited on at least three occasions: (1) date of initial location, (2) date of hatch to measure and mark chicks, and (3) several weeks after hatch to analyze nest site parameters. Many nests were revisited prior to hatch, but the number of visits was minimized to limit disturbance.

At each nest the number of eggs was noted and stage of incubation estimated by egg floatation (Westerskov 1950). Length and width of eggs were measured to the nearest 0.1 mm and in 1976 egg volumes were measured to the nearest 2.5 ml by water displacement. In two-egg clutches, larger-volume eggs were marked "1" with pencil and smaller-volume marked "2". In 1976, amount (little-moderate-much) and type of nest material were noted. Topographic features around the nest, plant species growing in and within a 1 m radius of the nest, distance to nearest open water, and elevation of the nest above water were recorded, and nests were photographed. Inter-nest distances were estimated from maps and aerial photographs of the study area.

Egg-hatching sequence was recorded when possible. Chicks were marked with serially numbered size 1 fingerling fish tags, applied in

the small web between the outer two toes of the right foot. Chicks in pipped eggs were similarly marked by breaking through the egg shell and withdrawing the foot, as described for ducks by Alliston (1975). Hatched chicks were weighed to the nearest gram with spring scales, and culmen, bill post nares, tarsus (diagonal and total) and middle toe (with and without the nail) were measured to the nearest 0.1 mm.

Banding

From 22 July through 21 August 1975 and from 20 June through 13 August 1976, cranes were banded and color-marked on and near the study area. A helicopter was available on 27 and 28 July 1975 and 9-13 August 1976 to assist in searching for and capturing chicks. Chicks spotted from towers, boats, or helicopters were pursued on foot. Flightless adults occasionally were captured from boats in rivers. Capture sites of birds were noted on maps. Birds caught on the study area were checked for web tags and their locations noted very specifically. Birds were marked with: (1) U.S. Fish and Wildlife Service standard bands (size 8) placed above the intertarsal joint (left leg 1975, right leg 1976), (2) 6.25 cm black-symboled yellow plastic bands placed above the intertarsal joint (right leg 1975, left leg 1976), and (3) black-symboled yellow aluminum collars fastened with pop rivets. Measurements made on each bird were: weight (nearest 25 gm), culmen, bill post nares, tarsus (diagonal and total), middle toe (with and without nail) and, on chicks, length of calamus and rachis of the ninth primary.

Distribution and Density

Aerial transects were flown on 27 June and repeated on 8 August 1976, in the area between the Keoklevik River to the north, mouth of the Tutakoke River to the south, Nuigalak Lake to the east and the Bering Sea to the west, covering an area of approximately 1,250 km^2 (Figure 2). Approximately 200 km of transect lines, 0.4 km wide, were covered, for a total area of about 80 km^2. Two gross habitat types--heath tundra (and mosaic tundra) and sedge/grass meadow--could be discerned from the 50 m altitude. The amount of time over each habitat type and crane group sizes seen in each were recorded.

Food Habits

Observations of feeding were recorded, and items taken identified in some cases. Gizzard contents from four cranes collected near the study area were examined and food items identified.

Captive-Reared Bird

In 1976 a crane chick was hatched and raised at the field camp. Its growth was recorded weekly, and notes made on plumage development, behavior and food habits (growth and plumage data not reported here).

Statistical Analyses

All statistical analyses were conducted according to Sokal and Rohlf (1969).

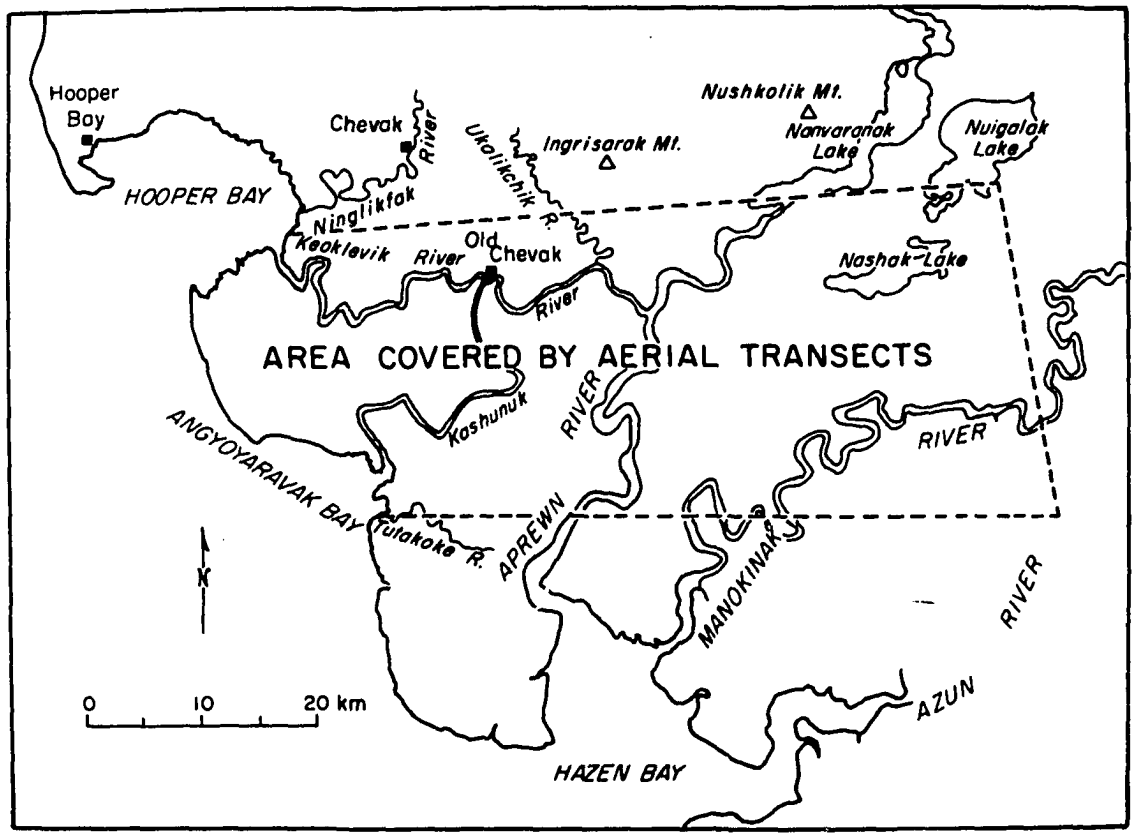

Figure 2. Portion of Yukon-Kuskokwim Delta covered by aerial transects.

RESULTS

Spring Phenology

Cranes were present on the study area by the first week of May in both years. At this time in 1975 (Petersen 1976) and 1976, ponds and rivers were covered with ice and at least 95% of the land area was snow-covered. Snow and ice melt occurred slightly later than average in 1975 and was delayed about one week in 1976 (James King, personal communication). This difference is reflected somewhat in May temperatures (Table 1). On 15 May 1976, a blizzard with winds to 60 knots or greater deposited fresh snow on the entire area. Nest-site availability and nesting activities were undoubtedly affected by this storm. By 14 May 1976, heath tundra areas were snow-free, and lower, marshier areas in heath tundra were beginning to appear. Snow deposited by the 15 May storm melted rapidly, so most heath tundra and some marsh areas were snow-free by 16 May. Low sedge/grass meadows were largely snow-free by 19 May.

Cranes were in pairs and flocks when I arrived on the breeding ground. Paired birds were apparently breeders, as they had established territories, while birds in flocks remained together and were considered nonbreeders, i.e. young birds, and, later in the season, unsuccessful breeders. Two groups of three birds each were observed in areas adjacent to the study area in 1976. In each, two birds were identified as paired on the basis of their unison call and the third bird was silent and submissive. These latter birds were probably

Table 1. Temperature data (°F), Old Chevak area.

	Average Minimum						Average Maximum					
Month	1970[1]	1971	1972	1973	1975	1976	1970	1971	1972	1973	1975	1976
May[2]	30.2	32.1	29.6	29.3	26.4	25.3	41.4	36.8	42.7	46.4	42.2	39.2
June[3]	37.1	39.9	40.6	39.3	34.0	33.0	56.1	47.2	51.4	50.5	52.6	52.3
July	44.2	45.3	49.0	43.9	43.2	42.2	53.0	54.3	62.5	58.8	60.4	59.9
August[4]	44.4	44.7	45.2	41.5	44.0	43.8	53.9	57.6	60.4	53.8	59.3	59.6

[1]Data for 1970, 1971, 1972 are from Mickelson (1973) and for 1973 from Dau (1974).

[2]Beginning 4 May 1970, 16 May 1971, 8 May 1972, 6 May 1973, 3 May 1975 and 2 May 1976.

[3]Temperatures from 1-16 June 1970.

[4]Temperatures from 15 days, August 1971.

chicks from the previous year, but no marked birds were seen to confirm this hypothesis. No similar three-bird groups were seen on the study area.

During the pre-nesting period, encounters between single, unidentified birds and one or both birds of territorial pairs were often observed. The single birds were possibly young non-breeders, exploring the area for available territories (Walkinshaw 1965d), and were driven off by display as described by Walkinshaw (1965d).

Territorial disputes were observed on only two occasions. In both cases, all birds displayed and/or danced. No physical combat was observed, and disputes were apparently resolved quickly.

On 6, 10, 12, and 23 May 1976, copulation was observed. All copulations proceeded as described by Walkinshaw (1953b).

Nesting Behavior

On 13 and 19 May two pairs were observed initiating nest building, in both instances on small snow-free grassy patches in a snow-covered meadow. Members of the pairs alternately sat on the potential nest. As one bird rose and left the nest, the other took its place. After up to one hour of this activity, the birds left the areas, one pair in response to a third bird's arrival and the other for no observable reason. Cranes assumed to be these pairs eventually nested in the vicinities of these sites, but neither pre-tested nest was used.

On 14 May, birds apparently with a nest were observed for two hours. Nest attendance duty was changed once during this period, and

the nest was sat upon constantly. The exchange was quiet and unceremonious. The relieving bird quickly settled onto the nest while the relieved bird slowly moved away. No nest-testing behavior similar to that seen on 13 and 19 May was seen. Although no eggs were seen, these were considered to be the first incubating birds observed. Later searching revealed no nest in this location, the nest having been destroyed or possibly abandoned during the 15 May blizzard.

During incubation, single, unidentified birds often visited nests under observation. Occasionally these birds were tolerated, but in most cases the non-incubating bird returned immediately to the nest and drove the intruder off by flying at it, or the intruder left the area upon seeing the mate approach. Incubation duty was exchanged after these disturbances. Cranes flying over the nest caused incubating birds to "hide" by crouching down with head and neck extended on the ground. These intruders were escorted out of the area, in the air, by the non-incubating bird.

Cranes were very attentive to their nests throughout the incubation period. No nest was observed unattended except when birds were forced off by human disturbance. In early incubation, birds ran from nests or sneaked away unnoticed when approached to a distance of 300 m or more. Later in the period, incubating birds sat tighter, and birds on pipped eggs or newly-hatched chicks could be approached to 30 m or less before flushing. These observations indicate that the cranes' attraction to their nests increased as incubation progressed, as

reported by Walkinshaw (1965a). After flushing, birds did not return to nests as long as I was within sight.

Nests and Nesting

Most nests were located on wet marsh sites in the mosaic habitat or in sedge/grass meadow. In 1975, eight nests in marshy areas were all located on some type of mound at least slightly higher and drier than the surrounding areas. One nest was found on a heath tundra ridge, overlooking a marsh and lake. In 1976, most nests were again slightly higher than the surrounding area but no truly heath tundra nests were found, although two nests were on islands which were quite dry and had some heath species on them. Of 20 nests on the study area in 1976, the mean distance to nearest open water was 6.0 m (range 0 to 50), and of eleven nests the mean elevation above water was 27 cm (range 5 to 60). Nests were located on seven types of topographic features: raised mounds in meadows (9), wet marsh meadows (4), narrow isthmuses between ponds (3), low wet islands (3), slough banks (2), islands in marshes (1) and dry islands in ponds (1). Dominant plant species around nests were *Arctagrostis latifolia*, *Festuca rubra*, *Elymus arenarius*, *Carex Lyngbyaei*, *C. rariflora*, *Betula nana*, *Empetrum nigrum* and *Sphagnum* spp. (plant names according to Hultén 1968). Plant species found at nest sites are summarized in Table 2.

Nest structure varied from inclusion of almost no lining material to massive mounds of vegetation. Amount of material was related to water levels. Those nests on drier sites not endangered by water

Table 2. Frequency of plant species within a 1 m radius of Lesser Sandhill Crane nests.

Species	Dominant		Present		Used in Nest	
	No. Nests	% Nests	No. Nests	% Nests	No. Nests	% Nests
Carex Lyngbyaei	6	30	9	45	8	40
Elymus arenarius	6	30	7	35	6	30
Sphagnum spp.	3	15	8	40	0	-
Carex rariflora	2	10	3	15	3	15
Festuca rubra	1	5	2	10	1	5
Arctagrostis latifolia	1	5	1	15	1	5
Empetrum nigrum	½*	3	4	20	0	-
Betula nana	½*	3	1	5	0	-
Potentilla Egedii	0	-	5	25	0	-
Rumex graminifolius	0	-	6	30	1	5
Salix ovalifolia	0	-	4	20	1	5
Chrysanthemum arcticum	0	-	3	15	0	-
Primula siberica	0	-	2	10	0	-
Eriophorum angustifolium	0	-	2	10	0	-
Carex Ramenskii	0	-	2	10	0	-
Poa arctica	0	-	1	5	1	5
Deschampsia caespitosa	0	-	1	5	0	-
Calamagrostis lapponica	0	-	1	5	0	-
Trientalis europaea	0	-	1	5	0	-
Polemonium acutiflorum	0	-	1	5	0	-
Ligusticum scoticum	0	-	1	5	0	-

Table 2. (continued)

Species	Dominant		Present		Used in Nest	
	No.Nests	% Nests	No.Nests	% Nests	No.Nests	% Nests
Potentilla palustris	0	-	1	5	0	-
Unidentified grass	0	-	3	15	1	6
Unidentified sedge	0	-	4	20	0	-

*Both species present in equal abundance at one nest.

level changes had little lining material and those in wet or marshy areas where fluctuating water levels might flood nests contained large amounts of material. All nests were constructed of dead plant material available from the immediate vicinity of the nest. In most, but not all, cases this dead material was from the dominant and/or secondary plant species in the area. Most material was, therefore, grass or sedge, but other materials included twigs of willow (*Salix ovalifolia*), unidentified woody roots, and old stems of *Rumex graminifolius*. Additional nest material was added to some nests in small quantities during late incubation.

Nesting density was 0.54 nests/km^2 in 1975 and 0.78 nests/km^2 in 1976 (Table 3). Distances between nests ranged from 277 m to 1,575 m in 1976 (Table 4). Also in 1976, one pair remained consistently territorial throughout the season but did not nest. Five 1976 nests were within 450 meters of 1975 nests, one as close as 70 meters.

No evidence of nest re-use was found. Once birds had begun incubating, they were tenacious. Disturbance was kept to a minimum and no desertion was definitely attributed to human interference, although three birds which were disturbed early in incubation or laying in 1975, and their eggs collected for another study, may have deserted their nests. Activity at the field camp apparently did deter birds from nesting, however. In 1976, three territorial pairs of cranes were active near the field camp, but were disturbed almost daily and moved away before nesting. Since they were not marked, I do not know whether they nested elsewhere.

Table 3. Lesser Sandhill Crane nesting densities.

	1975	1976	
		Early Incubation	Late Incubation
Study Area Size, km^2	16.6	26.9	29.6
Number of Nests	9[1]	21[2]	19
Nests/km^2	0.54	0.78	0.71

[1]Includes three nests which were destroyed by people before my arrival.

[2]Includes one nest which disappeared before location.

Table 4. Distribution within habitats and nearest-neighbor distance of Lesser Sandhill Crane nests, 1976.

Habitat Type	Mean Distance to Nearest Crane Nest (m)	Range	Number of Nests
Sedge/Grass Meadow	995.8 ± 216.0[1]	821-1,265	5
Heath Mosaic	574.6 ± 354.5	277-1,575	15

[1]Mean ± standard deviation.

Eggs

Mean egg size was 90.8 mm by 58.5 mm based on measurements of 46 eggs (Table 5). Volumes of 31 eggs ranged from 112 to 176 ml, with a mean of 153.8 ml (Table 6). Volumes were normally distributed (Komolgorov-Smirnoff test for goodness of fit, $p < 0.05$).

Cranes begin incubation with the first egg, which is produced about two days earlier than the second (Walkinshaw 1949). Eggs which hatch first are assumed to be laid first. In twelve two-egg clutches, one egg was significantly larger than the other (paired t test, $p < 0.05$). Only seven of these hatched both chicks, and hatching sequence was ascertained for only four clutches on which volumes were measured. In two, the smaller-volume egg hatched first, and in the remaining two the larger hatched first.

Clutch Size

Mean clutch size was 1.83 in 1975, 1.65 on the study area in 1976 and 1.61 for all 1976 clutches (Table 7). One egg disappeared in mid-incubation in each of two two-egg clutches in 1976. The agent which removed these eggs was not determined, but as the eggs were removed intact, mammalian predators were suspected. The largest avian predator in the area, the Glaucous Gull (*Larus hyperboreus*), is capable of carrying off whole loon (*Gavia arctica* or *G. stellata*) eggs (Petersen 1976), but crane eggs are sufficiently larger and gulls probably cannot carry them.

Table 5. Lengths and widths of Lesser Sandhill Crane eggs.

	Number of Eggs	Mean Length (mm) (Range)	Mean Width (mm) (Range)
Total	46	90.8 ± 4.2[1] (81.4-97.8)	58.5 ± 2.4 (51.5-63.0)
One-egg Clutches	11	88.5 ± 4.7 (81.4-96.4)	58.1 ± 3.2 (51.5-62.8)
Two-egg Clutches			
Larger Egg	17	92.2 ± 3.4 (85.5-97.1)	59.3 ± 1.8 (57.3-63.0)
Smaller Egg	18	90.2 ± 4.1 (84.1-97.8)	58.1 ± 2.3 (51.5-60.9)

[1]Mean ± standard deviation.

Table 6. Volumes of Lesser Sandhill Crane eggs.

	Number of Eggs	Mean Volume (ml) (Range)
Total	31	153.8 ± 13.0[1] (112-176)
One-egg Clutches	7	152.3 ± 21.4 (112-172)
Two-egg Clutches	24	154.2 ± 9.9 (142-176)
Larger Egg	12	159.1 ± 9.6 (146-176)
Smaller Egg	12	149.0 ± 8.0 (142-157)

[1]Mean ± standard deviation.

Table 7. Lesser Sandhill Crane clutch size frequencies and average clutch.

Clutch Size	1975	1976	
		Study Area	Total[1]
1	1	7	11
2	5	13	17
Mean Clutch Size Laid	1.83	1.65	1.61
Mean Clutch Size Hatched	1.45	1.50	
Number of Nests	6[2]	20	28

[1]Includes clutches observed both on and off the study area.

[2]Does not include three nests destroyed by humans during laying.

Hatching and Nesting Success

Hatching occurred from 16 June through 1 July in 1975 and 14 through 28 June 1976 (Table 8). One 1976 clutch due to hatch on 2 or 3 July was destroyed prior to hatching. Eggs in four two-egg clutches hatched one day apart, and in two they hatched two days apart. Hatching success was based on eggs. Nesting success was based on nests; a nest which hatched at least one egg was considered successful. Thus nesting success was 66.7% and hatching success was 63.6% in both years. Tables 9 and 10 summarize losses of eggs and clutches.

No predation was observed directly. Potential predators active on the study area include Parasitic and Long-tailed jaegers (*Stercorarius parasiticus and S. longicaudus*), Glaucous Gull, Mew Gull (*Larus canus*), red fox (*Vulpes fulva*), arctic fox (*Alopex lagopus*), mink (*Mustela vison*), and shorttail weasel (*M. erminea*) (mammal names according to Burt and Grossenheider 1952). Although the responsible predator could not be positively identified in most cases, if egg remains were present in or near the nest the predator was assumed to be a gull or jaeger, and if eggs had been removed intact, they were considered taken by mammalian predators. When disturbed, cranes may destroy their own eggs, in a pattern similar to other avian predators (Drewien 1973). Any eggs destroyed by cranes in this study were probably counted as destroyed by avian predators. In 1975, 36.4% of eggs were lost to predators, compared with 24.2% in 1976. Predation occurred prior to 15 June and after 25 Jule in 1976.

Table 8. Reproductive success of Lesser Sandhill Cranes.

	1975	1976	Total
Number of Eggs Laid	11	33	44
Number of Eggs Hatched	7	21	28
% Nesting Success	67	70	69
% Hatching Success	64	64	64
Hatching Dates	16 June-1 July	14-28 June	
Number of Nests	6	20	26

Table 9. Fates of Lesser Sandhill Crane eggs.

Fate	1975		1976		Total	
	Number	%	Number	%	Number	%
Hatched	7	63.6	21	63.6	28	63.6
Predators	4	36.4	8	24.2	12	27.3
Addled	0	-	4	12.1	4	9.1
Number of Nests	6		20		26	

Table 10. Fates of Lesser Sandhill Crane nests.

Fate	1975		1976		Total	
	Number	%	Number	%	Number	%
Hatched	4	66.7	14	66.7	18	66.7
Unsuccessful	2	33.3	6	28.6	8	29.6
Unknown	0	-	1	4.8	1	3.7

Renesting

Cranes which lost half-clutches seemed unaffected by the loss and continued incubating. Pairs losing whole clutches apparently did not renest, but remained on the nesting territory for two weeks or longer, responding to intruders by calling loudly and flying to some distant vantage point, but not leaving the territory. When the birds finally did leave the territory, they probably joined flocks of non-breeders.

Brood Season

In 1975, six chicks were web-tagged in five nests, and 16 in twelve nests in 1976. Measurements of these chicks are summarized in Table 11. Family groups were observed in both years from hatching to fledging and a family which fledged one chick in 1975 was observed regularly. Although this family was usually present near an observation tower from the time the chick was 23 days old, the birds spent much time along slough banks where vegetation (primarily *Elymus arenarius*) was taller than the chick and often taller than the adults, making observation difficult. The birds also used heath tundra and short-grass meadows, where their activities were more easily observed. Both adults fed the chick. Three methods of feeding were observed: (1) direct bill-passing of food items from adult to chick, (2) adults dropping food items on the ground in front of the chick, and (3) adults digging up patches of ground with the bill, in which the chick foraged. Frequency of feeding of chicks by adults appeared to decrease as chicks grew and fed themselves more, but adults were still giving chicks

Table 11. Measurements of Lesser Sandhill Crane chicks at hatch.

Measurement	Mean	Range	Number of Birds
Weight (g)	102.9 ± 10.9[1]	90-120	14
Culmen (mm)	20.9 ± 1.2	19.0-22.6	16
Bill Post Nares (mm)	14.8 ± 0.6	13.3-15.7	16
Diagonal Tarsus (mm)	41.5 ± 1.7	37.5-43.8	13
Total Tarsus (mm)	47.0 ± 2.2	43.0-48.7	14
Toe with Nail (mm)	31.5 ± 2.6	26.3-36.2	14
Toe without Nail (mm)	28.0 ± 1.5	25.2-31.0	12

[1]Mean ± standard deviation.

occasional food items in late August. Females fed chicks more frequently than did males in one-chick families, and chicks in these families tended to stay closer to the female than the male. In 1976, when two-chick families were observed briefly, both parents seemed to participate about equally in the feeding.

Survival of chicks to fledging on the study area was determined by recapture of marked chicks just prior to fledging (and, in a few cases, just after fledging), capture of unmarked chicks near nests in which eggs hatched but chicks were not marked, and observation of fledged chicks on known territories. In 1975, 57% of chicks which hatched on the study area survived to fledging, compared with 71% in 1976 (Table 12). In 1975, no two-chick families fledged both chicks, and no two-chick broods were seen. In 1976, two families on the study area fledged both chicks, and two-chick broods were common throughout the Delta. In both years, some chicks were captured and measured two or more times before fledging. Growth data on these chicks are summarized in Tables 13 and 14.

Throughout the pre-fledging period, families remained on territory and did not travel far from their nest sites. All recapture of chicks occurred within 610 m of nests, and all broods observed on the study area could be associated with known territories.

Banding

Twenty-one chicks were banded and 19 of these color-marked in 1975. Nine were captured with the aid of a helicopter; the remainder were seen

Table 12. Lesser Sandhill Crane chick survival.

	1975	1976
Number of Eggs Hatched	7	21
Number of Chicks Fledged	4	15
% Survival	57.1	71.4

Table 13. Summary of weight increases of Lesser Sandhill Crane chicks.

Web Tag Number	Age (Days)	Weight (g)	Age	Weight	Age	Weight	Age	Weight
3038	0	96	1	93	7	179	47	1,800
3039	3	126	44	1,900				
3042	12	355	30	1,200				
3046	0	114	58	2,350				
3050	0	120	53	2,700				
3063	0	90	53	2,200				
3065	0	94	53	2,700				
3069	0	112	41	2,250				

Table 14. Summary of culmen length increases of Lesser Sandhill Crane chicks.

Web Tag Number	Age (Days)	Culmen (mm)	Age	Culmen	Age	Culmen	Age	Culmen
3038	0	19.9	1	20.5	7	25.0	27	49.8
3039	3	24.5	44	55.7				
3042	12	29.1	30	43.0				
3046	0	20.7	58	61.7				
3050	0	22.0	53	62.4				
3063	0	20.4	53	57.8				
3065	0	19.5	53	63.5				
3069	0	20.8	41	55.9				

and pursued from boats or observation towers. At least three and probably more of the color-marked chicks lost their collars soon after capture in 1975, as collars were too large for some chicks. Collars were made slightly smaller in 1976, and retention was not a problem. In 1976, 71 birds were banded and color-marked. Two of these were adults, one flightless due to molt captured on 20 June and one with a wing injury captured on 19 July. Both were swimming in rivers and captured from boats. Seven chicks were caught from boats in 1976 and 62 from a helicopter. A few chicks flew away from the helicopter but landed after a short distance, apparently too weak or frightened to fly again, and were easily captured.

Three web-tagged chicks were recaptured and banded in 1975, and six in 1976. After banding, chicks immediately rejoined their parents. When later observed, marked chicks did not seem to suffer any discomfort or alienation due to their bands.

Nine color-marked birds were resighted during fall migration and on wintering grounds, and one bird banded but not color-marked was shot. Table 15 and Figure 3 summarize resighting information.

Distribution and Abundance

Table 16 summarizes data on distribution and density of the population at two seasons--hatching and fledging. In June, 69% of birds were seen in sedge/grass meadow, which comprised about half of the area transected, and in August, 74% of the cranes were in this habitat. These percentages are similar and indicate little or no

Table 15. Resightings of Lesser Sandhill Cranes marked on the Yukon-Kuskokwim Delta.

Collar No.	Date Marked	Date Sighted	Location
A30	28 July 1975	31 Oct. 1975	10 mi south of Roswell, N.M.
A31	15 Aug. 1975	12 Dec. 1975 15 Dec. 1975	Issaquena Co., Mississippi
A71	10 Aug. 1976	25 Oct. 1976	Rich Lake, Terry Co., Texas
A45	11 Aug. 1976	10 Nov. 1976	Bitter Lake NWR, New Mexico
A24	9 Aug. 1976	22 Dec. 1976 15 Jan. 1977 22 Dec. 1977	Lemitar, Socorro Co., N.M.
?	?(1976)	23 Oct. 1976	Pep, Hockley Co., Texas
?	?(1976)	5 Oct. 1976	Battrum, Saskatchewan
?	?(1976)	13 Feb. 1977 18 Feb. 1977 20 Feb. 1977	Rich Lake, Terry Co., Texas
?	?(1976)	13 Feb. 1977 18 Feb. 1977 20 Feb. 1977	Rich Lake, Terry Co., Texas

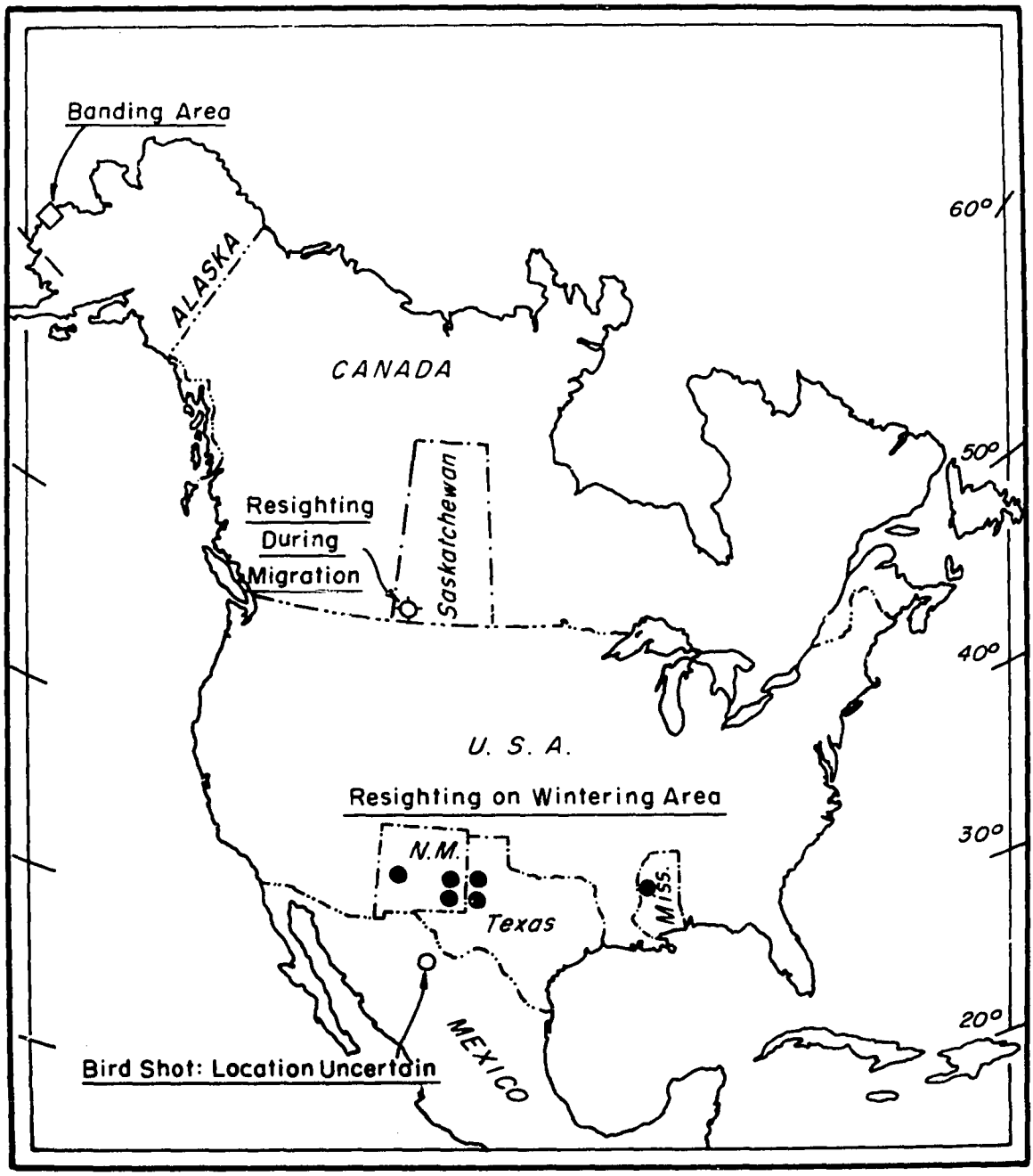

Figure 3. Locations of resightings of Lesser Sandhill Cranes marked on the Yukon-Kuskokwim Delta.

Table 16. Summary of Lesser Sandhill Crane sightings, by habitat type, from aerial transects.

Heath Tundra	
June	August
% Area: 48	% Area: 54
Adults: 45 (31%)	Adults: 26 (24%)
Chicks: 0	Chicks: 6
Total: 45 (31%)	Total: 32 (26%)
Sedge/Grass Meadow	
June	August
% Area: 52	% Area: 46
Adults: 100 (69%)	Adults: 84 (76%)
Chicks: 0	Chicks: 5
Total: 100 (69%)	Total: 89 (74%)
Summary	
June	August
Area: 93 km^2	Area: 80 km^2
Number of Birds: 145	Number of Birds: 121
Cranes/km^2: 1.56	Cranes/km^2: 1.51

change in distribution by habitat from June to August. Densities of cranes remained constant at about 1.5 birds per km^2.

Food Habits

Scattered observations of crane food habits were obtained in 1975 and 1976 from observations of feeding birds and gizzard content analyses (Table 17). Food items identified included crowberries (*Empetrum nigrum*), salmonberries (*Rubus chamaemorus*), microtines (probably *Microtus oeconomous* in most cases), small fish (probably *Pungitius pungitius*, P. G. Mickelson, personal communication), flying insects, and snails.

Table 17. Contents of gizzards of Lesser Sandhill Cranes collected near Old Chevak.

Age and Sex of Bird	Date Collected	Food Items Present
Immature Female	19 May 1976	fruit and seeds of *Empetrum nigrum*
Immature Female	11 August 1976	fruit and seeds of *E. nigrum* and *Rubus chamaemorus*
Adult Female	6 September 1976	seeds and fruit of *E. nigrum* and *R. chamaemorus*
		unidentified snails and snail shell fragments
		hair, bones and teeth of unidentified microtine
Adult ?	6 September 1976	fruit and seeds of *E. nigrum* and *R. chamaemorus*

DISCUSSION

Breeding Biology

Spring Arrival

Cranes arrive paired on breeding areas (Walkinshaw 1949). In Michigan, yearling Greater Sandhills (*G. c. tabida*) apparently return to breeding grounds with their parents (Walkinshaw 1949). Drewien (1973) reported that few breeding pairs of Greater Sandhills returning to Grays Lake, Idaho, were accompanied by yearlings. His observations of marked birds indicated that those yearlings returning to their "natal valley" arrived up to two months after the breeding birds. In the present study, no chicks marked in 1975 were observed in 1976. The three-bird groups in which one bird was probably a yearling indicate that some chicks return to breeding areas with their parents. However, single vagrant birds, probably yearlings, which visited nesting birds, became common during early incubation (i.e. mid- through late-May), possibly indicating delayed return of some yearlings.

Philopatry

Although few nesting cranes have been marked in an effort to ascertain philopatry, most researchers agree that cranes are strongly philopatric. Drewien (1973) observed marked birds reusing the same territory. Littlefield and Ryder (1968), Thompson (1970), Valentine and Noble (1970) and Walkinshaw (1949, 1965d, 1973) report that pairs may reuse the same territory for several years. In years when the Old Chevak area was not occupied during early spring, cranes

consistently nested on an island in a small pond near the field camp (C. P. Dau, personal communication). Cranes nesting on a territory about 1 km from the camp may have nested locally for some time, as the birds seemed accustomed to human activity and low-flying aircraft which alarmed more remote birds. On a third territory, birds used the same pond, and probably the same island in the pond, for nesting in 1974 (D. G. Raveling, personal communication), 1975 (M. R. Petersen, personal communication) and 1976. In all cases, birds were probably the same pairs each year, but birds were not marked to affirm this assumption. Proximity of 1976 nests to 1975 nests also supports philopatry, birds on the territories considered to be the same in both years. Reuse of territory and nesting area seems to be the rule on the Yukon-Kuskokwim Delta.

Nests and Nest Sites

Greater Sandhill Cranes, Mississippi Sandhill Cranes (*G. c. pulla*), and Florida Sandhill Cranes (*G. c. pratensis*) nest in shallow water or in very wet marshes (Walkinshaw 1949, 1965b, d, 1973; Drewien 1973; Valentine and Noble 1970; Hamerstrom 1938). Cuban Sandhills (*G. c. nesiotes*), however, nest on dry land, even on mountainous slopes (Walkinshaw 1953a). Canadian Sandhills (*G. c. rowani*) may nest in water but may also use drier sites. Drewien (1973) states that the Greaters nesting at Grays Lake, Idaho, tend to use drier sites than do other populations of that subspecies, and reports the mean distance to open water for land nests (44% of nests) is 4.6 m, slightly

less than the mean for all nests in the present study. In all cases, nests found on dry land consist of less material than nests in water. Lesser Sandhill nests have been reported from a variety of sites. On Banks Island, Northwest Territories, the birds nest on sand dune tops, using very little nest material (Walkinshaw 1965c). Walkinshaw (1949) states that, in general, Lessers nest in open tundra (i.e. heath tundra), near water. Near Johnson River, Alaska, Walkinshaw found four nests in heath tundra and one in wet marsh tundra (Walkinshaw and Stophlet 1949), while in the Chevak area all nests were on small knolls in the tundra (Walkinshaw 1950). Conover (1926) reported nests in the Hooper Bay area on raised mounds, apparently in wet marsh tundra. Similarly, Nelson (1887) found nests near the lower Yukon River in grassy flats (i.e. sedge/grass meadows) on slight mounds. The results of my study show wet marsh tundra and sedge/grass meadow to be the preferred nesting habitats in the Old Chevak vicinity, in contrast to Walkinshaw's findings. Heath tundra nests do occur, and these are probably more common further inland (e.g. the Johnson River area), where there may be less wet marsh and sedge/grass meadow available. As in other reports, the nests in my study were often on slight mounds in these marshes. None of these reports, however, indicated nests in standing water. Two such nests were found in 1976, and were built of large amounts of dead sedge, similar to nests of subspecies which typically build nests in shallow water. In general, the Lessers use drier sites than the other subspecies, except Cuban and possibly

Canadian Sandhill Cranes. The nests are, however, close to standing water if not in it. Sandhills in Siberia apparently nest in habitats similar to those described in the references cited above. Dement'ev and Gladkov (1951) reported Lesser Sandhill Cranes in Anadyr Territory nesting in wet, brush-covered tundra to elevations of 1000 m.

In all subspecies of Sandhill Cranes, nests are built of dead vegetation available from the immediate vicinity of the nest (Walkinshaw 1949, 1973; Drewien 1973; Valentine and Noble 1970; Thompson 1970). Thus the nest of the Cuban Sandhill is made of pine needles (Walkinshaw 1953a) while plant species found in other nests vary depending on surrounding vegetation. The variability of nest material is reflected in the number of species found in nests in the Old Chevak study area. In some cases, birds did seem to preferentially select the larger-stemmed plant species for nest building, rather than the dominant one, but always used vegetation immediately available.

Amount of material in the nest varied with wetness of the site in all reported cases. Littlefield and Ryder (1968) and Walkinshaw (1973) found material added to the nest when rising water levels threatened the eggs. In shallow-water nests in 1976, no evidence of such additions was seen, possibly because water levels in the marshes did not rise dangerously during the incubation period.

Walkinshaw (1965d) stated that "some type of cover is necessary" for a crane territory. Although many Sandhills nest in areas where they are not visually separated from one another, at least early in

season before new vegetation growth begins (Drewien 1973; Thompson 1970), other populations seem to require visual isolation (Walkinshaw 1965b). In the open, treeless tundra, the only barrier capable of visually separating cranes is the raised ridges of heath tundra which separate marshes and ponds in areas of mosaic habitat distribution. Perhaps these ridges do function as "cover," or visual barriers, isolating crane nests from one another. The inter-nest distance in mosaic habitat was significantly less than that in sedge/grass meadow (Student's t test, $p < 0.05$), indicating that birds may nest more densely in areas where the mosaic is such that small marshes are close together but separated by heath ridges. In the very flat meadows, nests were isolated by distance.

A primary factor influencing nest site selection must be snow cover. In mid-May, much of the nesting habitat is not open, and nest sites must be chosen from the snow-free areas. While heath tundra is available before marsh or meadow, the latter are chosen. Locations of snow-free patches in marshes and meadows vary from year to year, depending on weather conditions, so nest sites on the territory vary. Proximity of 1976 nests to 1975 nests, and reuse of nesting areas for three or more years, implies that philopatry and location of previous nests are important in determining the location of the nests. Vegetation around the nest does not appear to be as important in nest location as is proximity to water. However, the proximity to water may be a result of selection for preferred habitat types rather than

the presence of the water itself. When nests are built, the snow-covered marshes and ponds appear similar; thus a nest close to a snow-covered area may, after thaw, be close to a low but dry meadow or a pond. Generally cranes on the Yukon-Kuskokwim Delta appear to be able to utilize a variety of nest site types. Drewien (1973) suggested that use of dry-land sites by Greater Sandhills at Grays Lake may be related to egg predation, the predation rate being low in that study area. This may also be the case on the Yukon-Kuskokwim Delta. Egg predation was fairly low in 1975 and 1976, and mammalian predators were responsible for only part of egg loss. If nesting on islands is primarily a defense against mammalian nest predation, as shown for Cackling Geese (*Branta canadensis minima*) on the Yukon-Kuskokwim Delta (Mickelson 1973), and if nest predation by mammals is low, then use exclusively or preferentially of water sites may not be necessary. Nesting in water does not offer protection against avian predators, which may be as important as mammalian predators in the area.

Reuse of Nests

Florida and Mississippi Sandhill Cranes have been reported to use the same nest for more than one nesting season (Thompson 1970; Valentine and Noble 1970). On Banks Island, Northwest Territories, Walkinshaw (1965c) found evidence of reuse in two of four nests found. No evidence of reuse of nests was found in the present study. Cranes nesting on drier sites use little nest material and the energy expenditure in nest building is probably small. For these birds the

advantage of reusing an old nest may be outweighed by the disadvantage of the nest being under snow in some years. Larger nests, those in standing water for example, could be reused to the cranes' advantage. The two nests found in standing water in this study were the only raised structures for some distance, and would probably be available while the rest of the marsh in which they were found was snow-covered in early spring. Thus the probability of their being selected as nest sites in another year would increase.

Nesting Density

My late arrival on the study area in 1975 leads to difficulty in interpreting breeding biology parameters in that year. Also, my increased familiarity with the study area in 1976 may have affected results in this and other aspects of the study. If cranes are philopatric, then the number of territories on a given small area (e.g. the Old Chevak study area) should be approximately the same from year to year. The 1975 nesting density was calculated from the number of nests remaining on the area late in the incubation period, and is thus lower than the 1976 density. This is at least partly due to disappearance prior to location of some nests. Thus 0.54 nests per km^2 must be considered a minimum nesting density. By late incubation in 1976, at a time comparable to dates of nest location in 1975, the number of nests remaining on the study area was high (0.71 nests/km^2).

Egg Sizes

Although eggs in two-egg clutches were different in size, no conclusion can be drawn regarding a relationship between egg size and laying (and hatching) sequence. Egg size did not appear to be related to clutch size.

Clutch Size

Clutch sizes of Sandhill Cranes range from 1.7 in the Mississippi Sandhill (Valentine and Noble 1970) to 1.966 in the Greater Sandhill (Walkinshaw 1973) and the mean clutch size for all subspecies is 1.93, based on 574 clutches (Walkinshaw 1973). The mean clutch size on the study area in 1975 was comparable with other reports, but the 1.65 figure in 1976 was significantly lower ($X^2 = 34.56$, $p < 0.05$) than the mean reported by Walkinshaw. The low clutch size may have resulted partly from partial predation on nests. Several clutches were not located until mid-incubation, so the original complement of eggs produced was not really known. Such partial predation did occur in two nests on the study area in 1976, and was reported by Thompson (1970) to be responsible for some one-egg clutches in Florida. All one-egg clutches were located in mosaic habitat, as were the two nests from which one egg disappeared. Red foxes were most active in this habitat type. Factors other than partial predation must also be operating, since the lowest clutch size reported in another study was from a predator-free area (Valentine and Noble 1970). Also, in this study one pair of cranes which apparently nested in the same area in both years had a one-egg clutch in both years.

Egg and Clutch Loss

Predation, infertility and addled eggs account for most egg loss in Sandhill Cranes. Predation varies from 0% in Mississippi (Valentine and Noble 1970) to 52.7% in Oregon (Littlefield and Ryder 1968). The latter rate is high, with other reports of 10% (Drewien 1973), 9.1% (Walkinshaw 1973), and 11% (Thompson 1970). Predation rates during this study were intermediate, and were probably higher on the study area than off it in both years. Crane eggs are seldom left unattended (Walkinshaw 1965a), and repeated flushing of birds leaves otherwise-covered eggs open to predation. Also, any loss of eggs caused by the cranes themselves would undoubtedly be due to interference, as reported by Drewien (1973). In both 1975 and 1976, small rodents, primarily tundra voles (*Microtus oeconomus*) but also brown lemmings (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), were common on the study area. In 1975, microtines were seen almost daily, and in 1976 they were abundant. Predation on crane eggs and young may have been allayed to some unknown degree in both years by abundance of microtine prey. Eisenhauer (1976) reported that microtine abundance led to reduced predation on waterfowl young at Kokechik Bay (about 40 km north of Old Chevak) in 1973.

Infertile and addled eggs were not differentiated in this study, but were all recorded as addled for simplicity. No addled eggs were found in 1975, and 12.1% of the 1976 eggs were addled. This rate of addling/infertility is comparable with reports from other studies of

11.6% (Walkinshaw 1973), 17.5% (Walkinshaw 1949), 18% (Thompson 1970) and 3.5% (Drewien 1973).

Nest desertion is often related to human disturbance (Walkinshaw 1973; Valentine and Noble 1970). No cases of desertion were well documented in this study, but desertion may have occurred. The three nests found before my arrival in 1975 from which eggs were collected may have been disturbed enough to cause desertion before eggs were taken. Cranes observed incubating on 14 May 1976 may have deserted their nest as a result of weather. Another pair also observed incubating left its nest before I visited it, but I do not know whether the eggs were taken by a predator or the birds left the nest for some other reason. Flooding was a cause of nest loss in other studies (Walkinshaw 1973) but was not observed in the present study.

Hatching and Nesting Success

Reports of hatching success from other studies ranged from 62% of eggs (Valentine and Noble 1970) to 77% (Walkinshaw 1973), and the rate in this study each year was 64%. Nesting success ranged from 44% (Littlefield and Ryder 1968) to 88% (Thompson 1970). Values for 1975 and 1976 at Old Chevak were intermediate, and consistent from year to year. The 1975 values, however, must be considered maxima and were probably lower due to loss of eggs and clutches prior to my arrival on the study area.

Survival to Fledging

The variation in survival of chicks to fledging in 1975 and 1976

was the most striking difference in all breeding biology parameters. Even so, survival on the study area was possibly lower than on adjacent areas, due to disturbance of birds at critical times such as hatching. Factors possibly affecting survival, which differed in the two years, include weather and availability of alternate prey species. As indicated, microtine populations may have reduced predation on crane chicks. In Wood Buffalo National Park, Northwest Territories, Novakowski (1966) found that weather during May and June (i.e. nesting, hatching and early rearing periods) was critical to Whooping Crane (*Grus americana*) reproductive success, with low precipitation during the period being th ..ost important climatic factor affecting nesting success. In 1975, weather was wet, stormy and cool during the hatching and early brood-rearing period, while in 1976 this period was characterized by calm, warm days. Poor weather in 1975 may have prevented birds from feeding at critical times, subjected the vulnerable, newly-hatched chicks to exposure, or reduced the amount of food available. Most chick loss probably occurred during this period in both years.

Renesting

No good evidence of renesting was observed in this study. A chick approximately three weeks old banded near the study area on 12 August 1976 may have been produced by renesting or very late-nesting birds. Renesting has been reported in Greater Sandhills nesting in Michigan (Walkinshaw 1965b), in Oregon (Littlefield and Ryder 1968) and in Idaho, where renesting is possible if nests are destroyed prior

to mid-incubation (Drewien 1973). Mississippi Sandhills are also probably capable of renesting (Valentine and Noble 1970).

Non-Nesting Territorial Pairs

Young cranes may be mated and spend breeding seasons on territories and even build nests before they actually breed (Walkinshaw 1965d). One pair in this study defended a territory as did nesting birds, but throughout the season the birds were always seen feeding together, never incubating. Extensive searching of the territory revealed no nest, and these birds were assumed to be young non-breeders.

Productivity

A difference in productivity on the Yukon-Kuskokwim Delta in 1975 versus 1976 was evident and was reflected in higher survival of clutches to hatching and higher survival of chicks to fledging in 1976. During banding in 1975, broods were few and difficult to locate compared with 1976.

Recruitment was examined from two aspects in this study: (1) number of chicks fledged from the study area and (2) age ratios of birds observed during aerial transects made near fledging in 1976. The latter may be the less biased, as it covers a larger area, represents a larger sample size and allows inclusion of itinerant flocks of non-breeders and unsuccessful breeders which were not consistently present on the study area. However, aerial censuses in Idaho did not count all birds on an area, and higher percentages of chicks than

adults were missed, giving age ratios misleadingly high in adults (Drewien 1973).

Four chicks were fledged from nine pairs on the study area in 1975, and fifteen from 22 pairs in 1976, yielding study-area populations composed of 19% and 25.8% chicks in 1975 and 1976, respectively. In both years, flocks of 50 to 90 cranes used the study area during parts of the breeding season. If these are included as birds supported by the area, the percentages drop to 3.3%-5.6% in 1975 and 9.4%-13.8% in 1976. Since the birds in flocks were only partly supported by the study area, intermediate percentages probably represent the situation more accurately, but the proportion of resources these birds received from the study area is not known.

Eleven of 122 cranes seen during aerial transects on 8 August, or 9% of birds, were chicks. This percentage may be a low estimate, due to age-specific visibility bias. Young made up 3.1% to 11.5% of birds observed in surveys in the Central Flyway, where Lesser and Canadian Sandhills from a wide geographic range occur during migration (Table 18).

Mean brood size is another indicator of productivity. This figure does not express overall recruitment as it does not take into account lost broods, but it is convenient for comparative purposes and does indicate relative chick survival from year to year. During 1975, no two-chick broods were seen, so the mean brood size for that year was 1.0. Mean brood size was calculated in three ways in 1976. First, of 13 families on the study area, mean size of broods was 1.15. If

Table 18. Age ratios of flocks of Lesser and Canadian Sandhill Cranes in the Central Flyway.

Year	% Young[1]	Source
1966	4.3	Miller and Hatfield 1974
1967	5.9	Miller and Hatfield 1974
1972	3.1	Miller and Hatfield 1974
1973	5.3	Miller and Hatfield 1974
1974	11.0	Gollop 1976
	10.9	Buller 1975
1975	10.5	Gollop 1976
	11.1	Buller 1976

[1]Age composition of these flocks varies with time, so counts made in 1966, 1967, 1972 and 1973 may under estimate the proportion of young, since they included only part of the migration period (Gollop 1976).

disturbance during the study caused reduced survival of chicks on the study area, this figure may be biased. Including three broods observed immediately adjacent to the study area, mean brood size was 1.28. Of 69 chicks banded, mean brood size was 1.25. Most of these chicks were captured with the aid of a helicopter, which caused all birds to be very alarmed, and to flush or hide. In at least two and probably more cases, chicks banded as single-chick broods had siblings which were not seen at capture but were observed later. Thus the mean brood size of 1.25 must be considered a minimum figure. Third, from aerial transects, eight broods observed had a mean brood size of 1.38. This is probably the least biased of all mean brood size estimates, but is based on a small sample. Mean brood size during 1976 was at least 1.30 and may have been as high as 1.38.

Walkinshaw (1973) summarized brood sizes of Greater Sandhills in Michigan, where mean brood size over a 21-year period was 1.4, based on 1 to 33 broods per year. Miller (1973) stated that Lesser Sandhill Cranes seldom rear more than one young, referring to his observation of only one two-chick family in 623 family groups observed at Last Mountain Lake, Saskatchewan, during the fall of 1972. This is in contrast with the 1976 findings on the Yukon-Kuskokwim Delta, where two-chick broods were common. Productivity does apparently vary considerably, at least locally, from year to year.

Distribution and Abundance

During aerial transecting, the plane may cause birds to hide or to flush from the strip of land being examined, thus decreasing the number of birds seen. Visibility of birds is also affected by the habitat, the birds being readily visible against the green color of sedge/grass meadows but less so against brown heath tundra. For these reasons, data from aerial transects may be somewhat biased.

Crane density, which included non-breeding flocks as well as breeding birds, remained constant over the summer period at about 1.5 birds per km^2. If nesting density in 1976 was 0.78 pair, or 1.56 adults per km^2, this represents a density similar to that indicated by transects, without inclusion of non-breeders. The Old Chevak study area represents such a small portion of the area transected that nesting density on it may differ from that on the entire area. However, Drewien (1973) found his aerial observations revealed only 36%-71% of adults and 17%-23% of chicks known to be on an area in July. Thus it may be safe to assume aerial transects on the Yukon-Kuskokwim Delta were similarly biased and densities were higher than indicated by transect data.

Aerial transect data show no change in habitat use over the period studied. In both June and August, most birds seen were in sedge/grass meadows. Observations during summers of 1975 and 1976 indicated that birds did use sedge/grass meadows extensively at all seasons, but use of heath tundra areas increased in late summer,

probably in response to availability of berry crops. Nelson (1887) observed that the birds began frequenting berry-laden heath tundra in late July and during August. The date of transecting in August may have been too early to show the increase in use of heath tundra, which continued to increase as berry crops continued to ripen during August. Also, differential visibility may have prevented many birds in heath areas from being seen.

Food Habits

Most information on Sandhill Crane food habits comes from studies and observations of the birds during migration and on the wintering grounds. Other reports are fragmentary. No thorough analysis of crane feeding habits during the summer period has been conducted.

Walkinshaw (1949) stated that cranes are omnivorous, and habits vary considerably with season and with individual birds. Cranes have been reported to eat a very wide variety of items, both animal and vegetable. Although largely granivorous during fall and winter, cranes seem to become more carnivorous during summer. Greater Sandhills feed on plant material in spring, but as summer progresses, consume earthworms, other invertebrates, frogs, snakes, and even young blackbirds (Walkinshaw 1973; Hammerstrom 1938). Littlefield (1976) observed Greater Sandhills on the breeding grounds feeding on Gadwall (*Anas strepera*) and Mallard (*A. platyrhynchos*) ducklings, and Drewien (in Littlefield 1976) has seen them kill and eat Mallard and Green-winged Teal (*A. crecca*) ducklings. Harvey et al. (1968) reported Lesser

Sandhills feeding on eggs and young of Snow Geese (*Anser hyperborea*), Willow Ptarmigan (*Lagopus lagopus*), and, in one case a collared lemming.

Nelson (1887) reported that Lesser Sandhills in the St. Michaels (Alaska) area fed on crowberries from the previous summer and occasionally mice or lemmings during spring. Walkinshaw (1973) considered browsed vegetation to constitute the majority of spring food for cranes in Alaska and Banks Island. The one bird collected in spring near Old Chevak had eaten crowberries. Habitat utilization throughout the summer is also an indicator of feeding habits. Many birds were observed during May actively hunting, killing and consuming microtines. Microtines were apparently an important food item during this pre-breakup period. Similar observations were made during summer 1976 on Banks Island (J. Reed, personal communication). During this time, cranes used snow-free grass patches in wet tundra, where microtines were concentrated. As grasses and sedges began to grow tall, cranes continued to feed in flat meadows and along pond and slough edges. Pairs with chicks also fed in these areas and especially in stands of *Elymus arenarius* along slough banks, during the early rearing period. By late July, birds began increasing use of heath tundra, and by late August much feeding occurred in these areas rich in fruit of crowberry and salmonberry.

The captive chick expressed an early preference for meat and consumed microtines and small birds, including the fur, feathers and bones, as well as the flesh of many other species, including

fish, chicken and beef. He was also fond of craneflies, midges, mosquitoes, and other invertebrates, and was adept at catching them. In mid-August, however, his food preference changed. He became less fond of meat, preferring vegetable food, including primarily crowberries and on one occasion flowering heads of *Calamagrostis* sp.

Eggs and young of other bird species are abundant during much of the nesting season of Lesser Sandhill Cranes. Although I have never seen cranes kill ptarmigan chicks or other young birds, I do not doubt that they would if the opportunity presented itself. Such acts would be easy to overlook if the birds were in tall vegetation.

Although it is known that both adults feed the chicks, the amount of food provided by adults and the items fed to the chicks have not been investigated. Observations made during this study show that frequency of feeding by adults decreases as the season progresses and chicks feed themselves more. However, newly-hatched and very young chicks were not observed, and food items can seldom be identified, if seen at all, when birds are feeding at some distance.

Banding Success

Although only slightly more helicopter time was used in 1976, many more birds were banded than in 1975. This may have been partly due to banding dates which were slightly later in 1976, making chicks more visible and to improvement of technique, but success was also affected by the larger number of chicks present in 1976.

Migration and Wintering Areas

Most of the cranes from Alaska apparently enter the Central Flyway, passing through the Last Mountain Lake area in south-central Saskatchewan and the Kindersley district in the west-central part of the province (Gollop 1976). The pathway the Lesser Sandhill Cranes follow to the wintering areas has been described by Buller (1967, 1975, 1976), Johnson and Stewart (1973) and others. Resightings of birds in the present study support these findings, showing concentrations wintering in eastern New Mexico and western Texas (Figure 3). Chicks were all marked within 30 km of one another, yet some moved to wintering areas separated by several hundred kilometers. The occurrence in Mississippi of a Sandhill Crane banded on the Yukon-Kuskokwim Delta is very unusual. Perhaps the parents of this chick were killed along the migration route, or the chick became otherwise separated from them, and thus the chick's migration was affected. None of the marked Lesser Sandhills from the present study has been resighted in California, where from 500 to 10,000 Lessers usually winter in San Luis Obispo County (Walkinshaw 1973).

MANAGEMENT IMPLICATIONS

Lesser Sandhill Cranes probably comprise the vast majority of the hunted crane population (Wilson Ornithological Society 1975). Monitoring and careful management of this subspecies is particularly important. Nonconsumptive uses of cranes, such as birdwatching and enjoyment of the large flocks at congregation areas and during migration, should also be considered important reasons for maintaining the population at its current large size and stable level. These long-lived birds probably do not usually breed until they are three years old or older, although age of first reproduction has not been well investigated (Walkinshaw 1973), and are characterized by low reproductive rates relative to other game bird species. Human activity above minimal levels appears incompatible with crane nesting, as reflected in nest desertion as a result of human disturbance and displacement of territorial birds due to human activity. Loss of nesting habitat as a result of land development is a further threat to the population's stability.

Miller et al. (1972), Drewien (1973), Wilson Ornithological Society (1975) and others have outlined recommendations for Sandhill Crane management. Although some problems identified, such as crop depredations by cranes, do not relate directly to this study, these authors point out the need for protection of nesting areas, assessment of annual productivity and recruitment, better estimates of hunting pressure and hunter harvest in all areas, and better estimates of the size and place of origin of hunted populations. The following

discussion includes recommendations for achieving these goals with respect to the Sandhill Cranes on the Yukon-Kuskokwim Delta specifically, and Lesser Sandhill Cranes in general.

On the Delta, extensive aerial surveys conducted in mid- to late-August should give estimates of recruitment. Data thus obtained may be biased by age-differential visibility of birds, but by fledging, chicks are probably nearly as visible as adults. If conducted annually, relative productivity from year to year could be assessed. Determination of age ratios of flocks at fall and winter concentration areas is also desirable, since these flocks include birds from other populations of Lesser Sandhills and Canadian Sandhills.

In order to determine overall production of Sandhill Cranes from the Yukon-Kuskokwim Delta, an estimate of the total population on the area should be used in conjunction with estimates of recruitment rates. The population of Lesser Sandhill Cranes is considered to be stable (Wilson Ornithological Society 1975) and estimating the size of the population on the Delta at intervals of one to several years will provide valuable information for documenting increases or decreases in the population. Aerial surveys conducted early in the breeding season (i.e. early May) when the ground is still snow-covered and cranes are probably most visible, could be used to derive these estimates.

Nesting areas should be as free of human disturbance as possible. Much of the range of cranes on the Delta is on existing refuge and proposed refuge additions. The size of the crane population on

these areas should be estimated in order to assess the degree to which the population is protected by existing and proposed land classifications. Other breeding and/or nonbreeding concentration areas in the state should be identified and protected. Crane populations should be considered if development is proposed in these areas.

The current study, and studies on other subspecies, have contributed to knowledge of the biology of the Sandhill Crane, but further research is needed in areas touched minimally or not at all by these studied. Banding should continue, to provide marked birds for further investigation of initial breeding age and age-specific productivity, philopatry, specific migration patterns and wintering areas, and amount of interchange among breeding populations. A major emphasis of further research on breeding grounds should be examination of factors affecting productivity. Included in this objective should be the following: evaluation of effect of weather on nesting and rearing success; examination of predation on crane eggs and young versus alternate prey availability; assessment of summer food habits, especially of chicks, and of food availability and possible variation from year to year; determination of time and causes of chick mortality; investigation of relationships between chicks and between chicks and adults in two-chick broods; and investigation of renesting.

Even in the best years, crane reproductive rates appear to be low. Drewien (1973) observed 13-14% juveniles in fall flocks of a population of Greater Sandhills which was increasing in numbers. Littlefield and Ryder (1968) reported 9-11% juveniles in a stable population

of Greater Sandhills. Age ratios of fall migrant Lesser and Canadian Sandhills obtained in the Central Flyway in 1974 (Buller 1975; Gollop 1976) and 1975 (Buller 1976; Gollop 1976) and of Lesser Sandhills on the breeding ground in this study are comparable to the latter figures. The present study further indicated that productivity may vary considerably from year to year. Overharvest must be prevented. Harvest allotments must take into consideration this low annual recruitment and must also allow for annual variation in recruitment.

SUMMARY AND CONCLUSIONS

Breeding biology of the Lesser Sandhill Crane was studied during 1975 and 1976 at Clarence Rhode National Wildlife Range on the Yukon-Kuskokwim Delta, Alaska, the most important crane breeding area in the state.

Cranes were present in territorial pairs and nonbreeding flocks by the first week of May. Some young from the previous year may return with their parents, and others may arrive about one week later. Lesser Sandhills are probably philopatric as are other subspecies; cranes apparently reused territories and general nest areas but no reuse of nests was observed. Little territorial conflict occurred.

Two gross habitat types--heath/marsh mosaic and sedge/grass meadow--comprised the study area. A total of 26 nests was found on the study area, most on slightly raised mounds in wet marshes in the mosaic tundra and in sedge/grass meadows. Nest sites ranged from shallow water to dry heath tundra, and were generally drier than those used by Greater, Florida and Mississippi Sandhill Cranes. Nests averaged 6.0 m (range 0 to 50) from open water, and nest structure varied with wetness of the nest site. Nests were constructed of dead vegetation available at the nest site.

Nesting density was 0.54 nests/km^2 in 1975 and 0.78 nests/km^2 in 1976. Inter-nest distance ranged from 277 meters to 1,575 meters and was significantly shorter in heath/marsh mosaic than sedge/grass meadow. Raised heath tundra ridges in mosaic tundra may function as visual barriers separating cranes and allowing closer nesting than in

more open habitats. Mean clutch size was 1.83 in 1975 and 1.61 in 1976. Partial predation on clutches may have influenced the low clutch size in 1976. Hatching occurred from 14 June through 1 July, with one or two days separating hatching in two-egg clutches. Mean clutch size hatched was about 1.5 in both years. Egg size did not appear to be related to hatching sequence. Hatching success was 63.6% and 9.1% of eggs were infertile or addled. Nesting success was 66.7% and predators took 27.3% of eggs. Predation may have been allayed to some degree by abundance of alternate prey. No firm evidence of re-nesting was seen. Human disturbance may have caused some nest desertion in 1975, and did cause birds to leave territories before nesting in 1976.

In one-chick broods, females fed and attended chicks more than males, while the two parents participated about equally in these duties in two-chick broods. Families remained on territories throughout the brood season. In 1975, 57% of chicks survived to fledging, and 71% were fledged in 1976. Mean brood size was 1.0 in 1975 and about 1.3 in 1976. Most chick loss probably occurred during the early rearing period and in 1975 may have been increased by poor weather and its affect on food and feeding opportunities. Juveniles comprised 3-6% and 9-14% of birds supported by the study area in 1975 and 1976 respectively. In 1976, aerial surveys indicated densities of 1.5 cranes/km^2 over a 1,250 km^2 area, but this was probably a low estimate due to biased visibility of cranes from the air.

Both breeding and nonbreeding birds used low wet areas extensively throughout the summer, but increased their use of heath tundra in August as berry crops ripened. Food items included a variety of plant and animal material.

Ninety chicks and two adults were banded, and most of these were color-marked. Birds were captured primarily with the aid of a helicopter. Nine resightings of color-marked birds were reported during fall migration and from wintering areas, and one banded bird was shot by a hunter. Information from resightings indicates that birds from the Delta pass through southern Saskatchewan and winter primarily in eastern New Mexico, northwestern Texas and northern Mexico. No birds color-marked in 1975 were resighted on the breeding area in 1976.

The Lesser Sandhill Crane population is considered to be stable, but reproductive rates are low and over-harvest, loss of habitat, and undue disturbance on the breeding ground must be prevented. Further research, including banding, investigation of reproductive potential of known-age birds, amount of variation in productivity and factors affecting productivity, is essential for better understanding of Sandhill Crane biology and management of the species.

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